

information on length of moult in this species, other details are apparent. The sequence of moult appears to be normal for a passerine. Primary moult occurs first, with secondary, tertial and tail moult starting when primary moult is 30%–40% completed. Both adult and first year birds appear to undergo a complete moult in the autumn, as in the Common Snow Finch, and the timing of moult of both Theresa's and Common Snow Finches at this locality appears to coincide almost exactly (Table 2), indicating the same response to closely similar ecological requirements.

TABLE 2

Moult scores of Common Snow Finches *Montifringilla nivalis* caught at Band-i-Amir, Afghanistan. (Conventions as in Table 1.)

Primary	Moult scores (as a %)		Tail	Contour moult
	Secondary	Tertial		
56	0	0	37	—
50	3	27	10	—
42	0	13	0	xx
68	13	73	73	x
46	0	47	10	0
76	13	87	73	x
56	7	53	30	x
36	0	40	10	x
54	3	53	10	—
54	7	40	43	xx

*Acknowledgements:* The Oxford University Ornithological Expedition to Afghanistan and Kashmir 1970 was financially supported by numerous organisations and individuals. We wish to express our thanks to all of these.

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## Notes on the biology and systematics of Polynesian swiftlets, *Aerodramus*

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Received 15 November 1977

Swiftlets of the genus *Aerodramus* (formerly placed in *Collocalia*, but see Brooke 1972, Medway & Pye 1977) are widespread in the tropical Pacific Ocean from Australia and New Guinea east to the Cook, Society and

Marquesas Islands. Some of the larger islands of the southwest Pacific have two or three coexisting species, but only one species occurs on each island from Fiji east to the Marquesas. No other Apodidae breed on islands in the central Pacific and the only swallow (Hirundinidae) is *Hirundo tabitica* which breeds from Australia east to Tahiti.

Mayr (1937) describes the slight differences in morphology and coloration which separate some sympatric species of *Aerodramus*, and the consequent difficulties in judging affinities of allopatric populations which show small but constant differences from each other. Simms (1961) and Medway (1966, 1975) have since improved our taxonomic understanding of swiftlets by showing that the type of nest built and the ability or inability to echolocate may be useful in judging affinities. This paper discusses the swiftlets of southeast Polynesia from Tahiti, Atiu and the Marquesas Islands. They are more similar to each other in morphology than any one of them is to forms occurring further west in the Pacific. Atiu (20° 00' S, 158° 07' W) is about 750 nautical miles WSW of Tahiti and Moorea (17° 40' S, 149° 05' W), and 1260 nautical miles southwest of the nearest of the Marquesas Islands (9° 23' S, 140° 06' W), whereas Tahiti is only about 630 miles southwest of the Marquesas.

Mayr (1937) pointed out that the swiftlets of Tahiti (*C. l. leucophaea*) and the Marquesas Islands (*C. l. ocista*) agree in being rather large and dull coloured, with little or no trace of the pale supraloral spots found in some related species. They also have rather long tails and a distinctive soft texture to the plumage, although the texture is difficult to detect in old museum skins. A swiftlet discovered on Atiu in the southern Cook Islands in 1973 and given the name *Collocalia sawtelli*, has similar features (Holyoak 1974a). These features set the swiftlets of southeast Polynesia somewhat apart from the rest of the genus, but they appear to be closer to those of *A. vanikorensis* than of other Melanesian species.

duPont (1976: 106) synonymized *sawtelli* with *leucophaea*, stating that it is "Morphologically indistinct (specimens examined) but alleged to differ from *C. l. leucocephala* (sic) by echo locating". However, he could only have seen one specimen of *sawtelli*, a paratype lodged at the British Museum (Natural History), while the only comparative material available there consists of two old and faded specimens of *A. leucophaeus*. The differences between *A. sawtelli* (8 specimens examined), *A. leucophaeus* (12 specimens) and *A. ocistus* (92 specimens) in morphology and nest structure are summarized below.

### *Morphology*

Fully-grown birds of all populations of the *A. leucophaeus* group have predominantly blackish-brown upperparts with slightly paler underparts and a small light patch on the longer uppertail-coverts where light grey-brown feather bases are partly exposed. The pale patch is least conspicuous because the feather bases are darkest in birds from Tahiti and most conspicuous in those from Atiu, Marquesan birds being variable but usually intermediate. In fresh plumage there is a slight green gloss on the dark feathers of the upperparts and wing-coverts, but this disappears in old specimens, which become lighter and browner. Tahiti birds are lighter and browner than those from the Marquesas Islands, to judge from comparison of 50 year old skins of both, and the Marquesan specimens appear slightly lighter than three year old skins

from Atiu. The underparts of Atiu birds appear to be slightly but consistently lighter than in the other populations. To judge from museum skins, the feet and especially the claws have little dark pigmentation in Tahiti birds, more in Marquesan birds and most in Atiu birds.

TABLE I  
Measurements (mm) of wing and tail length in Polynesian swiftlets. There is little if any sexual dimorphism in size.

	<i>N</i>	<i>X wing</i>	<i>X tail</i>	$\frac{X \text{ tail}}{X \text{ wing}} \times 100$
Atiu	8	118.1 (s=1.22)	54.6 (s=1.08)	46.6
Tahiti	10	126.1 (s=2.02)	57.4 (s=2.19)	45.5
Marquesas Is.:				
Eiao	6	119.1 (s=1.73)	61.4 (s=2.01)	51.5
Nuku Hiva	37	122.4 (s=1.89)	62.6 (s=1.16)	51.2
Ua Huka	12	121.6 (s=1.28)	60.5 (s=1.37)	49.8
Ua Pou	5	127.4 (s=1.56)	66.3 (s=1.92)	52.0
Hiva Oa	21	123.1 (s=1.41)	62.8 (s=1.89)	51.0
Tahuata	4	121.7 (s=2.01)	62.3 (s=1.17)	51.2

*X*=mean. *s*=standard deviation.

Table I gives measurements of wing and tail length in each of the Polynesian swiftlet populations. Wing-length was measured by flattening the wing and straightening the primaries, tail-length was measured from between the bases of the central pair of rectrices. Tahiti birds are rather large with a relatively short tail, Atiu birds are small with a short tail and Marquesan birds are variable in size, but mostly rather large, and have relatively long tails. These differences in proportions may be related to differences in feeding behaviour. The short-tailed swiftlets of Tahiti differ from the others in tending to feed mainly above the forest, although they sometimes descend to feed amongst the forest canopy. In contrast, Atiu and Marquesan swiftlets more often feed by flying slowly among the twigs and branches of the forest edge and canopy (Holyoak & Thibault, in prep), so their higher tail/wing ratio may confer greater manoeuvrability when feeding in this way. That the Tahiti swiftlet tends to feed higher than the other swiftlet species may be associated with the presence of *Hirundo tabitica* on Tahiti but not on the other islands. *H. tabitica* mainly feeds close to the forest canopy or edge or over water and it has a much longer tail than any of the swiftlets. Further, flycatchers which catch prey on the wing are absent from southeast Polynesia and this may be associated with the fact that most *Aerodramus* and the *Hirundo* of the region commonly feed very close to forest trees. Samoa and Fiji do have flycatchers which catch prey on the wing (e.g. *Myiagra* spp.) but the swiftlets there (*A. spodiopygius* subsp.) habitually feed at some height above the ground and rarely enter the forest edge or canopy, and the Fijian populations of *Hirundo tabitica* differ from the Tahiti population in infrequently feeding amongst the forest canopy or at the edge.

The structure of the bill varies between different swiftlet populations in southeast Polynesia. In Tahiti birds the maxilla is heavy with a short hook and it is not abruptly attenuated towards the tip. In Atiu birds it is weaker with a rather long hook and abrupt attenuation distally. Marquesan birds are intermediate between those of Atiu and Tahiti.

The Atiu swiftlet appears closer to the Marquesan swiftlets in coloration and various morphological features than it does to the Tahiti swiftlet, although it resembles the latter in having a relatively short tail.

#### *Nests and nest sites*

Unfortunately, very little information is available on the nests and nest sites of the Tahiti swiftlet. Wilson (1907) reported seeing nests on a rocky crag, and Quayle (MS., in Holyoak 1974b) saw nests made of moss in a shallow depression in a rocky crag. It is uncertain whether this Tahiti swiftlet, which is now considerably reduced in numbers, has the ability to echolocate, although echolocation would be unnecessary in the nest sites that have been described. The absence of native hawks and owls from southeast Polynesia may have allowed swiftlets there to nest more openly than the native hawks present on islands of the southwest Pacific would allow; and the introduction of the Indian Mynah *Acridotheres tristis* to the Society Islands and Hiva Oa might have been at least partly responsible for the decrease of swiftlets there.

Marquesan swiftlets nest in colonies of from two or three to a hundred or more nests in very varied sites. Some are in shallow depressions under overhanging rock crags or sea cliffs, others are in shallow caves and others are in deep caves. The more open sites receive full illumination, others are partly illuminated and some colonies in true caves receive no light at all. Holyoak (1974a) thought that Marquesan swiftlets do not echolocate, but recent studies have shown that in deep caves flying birds utter series of distinctive rattling clicks which are quite different from the calls used outside caves, and which almost certainly function in echolocation (cf. Griffin & Suthers 1970).

The nests of Marquesan swiftlets are substantial cup-shaped structures built mainly of pleurocarpous mosses collected from trees, sometimes with the addition of small amounts of lichen and fibres of higher plants (Fig. 1). The nest materials are cemented together with small quantities of sticky transparent saliva and the mossy cup often contains a variable number of swiftlet feathers. The nests are normally stuck to vertical or slightly overhanging rock, even though small ledges are often present close by.

The Atiu swiftlet nests only in deep caves in the uplifted coral limestone of the makatea region of the island. A colony visited in the Anataketake Cave in September 1973 contained c. 60 nests and local people reported that there were a few smaller colonies in similar caves elsewhere on the island. Some nests received a little light from the cave entrance, but most were in complete darkness. Distinctive rattling clicks were given continually by birds flying in dark parts of the cave, but these were not heard outside. There can be little doubt that these clicks function in echolocation.

The nests of Atiu swiftlets were found only on small ledges high up in the cave. They were shallow cup-shaped structures woven from plant fibres, lichens or both, that were cemented together with quantities of sticky transparent saliva (Fig. 2). Some of the 20 nests inspected were so flimsy



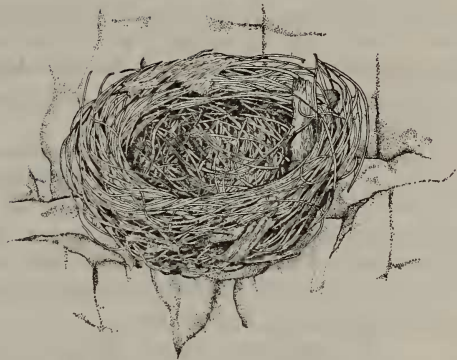


Figure 1 (Left). Nest of *Aerodramus (leucophaeus) ocistus* collected on Ua Pou, Marquesas Islands, October 1975; specimen in Brit. Mus. (Nat. Hist.).  $\frac{1}{2}$  natural size. Drawn by Mrs. Linda Whitehouse.

Figure 2 (Right). Nest of *Aerodramus (leucophaeus) sawtelli* collected on Atiu, southern Cook Islands, September 1973; specimen in Brit. Mus. (Nat. Hist.).  $\frac{1}{2}$  natural size. Drawn by Mrs. Linda Whitehouse.

that the egg rested on bare rock within the cup and in most nests there was only a thin layer of plant fibres beneath the egg. Moss and feathers were absent from all the nests inspected.

Eggs of the Atiu swiftlet are apparently smaller than those of Marquesan swiftlets in conformity with the smaller size of adult birds from Atiu. Four eggs from Atiu measure  $17.4 \times 12.6$ ,  $17.9 \times 12.7$ ,  $18.1 \times 12.6$ , and  $18.0 \times 12.8$  mm, whereas one from Nuku Hiva, Marquesas Islands measures  $21.8 \times 12.5$  mm.

### Taxonomy

It is difficult to decide on the best taxonomic treatment for the *Aerodramus* of southeast Polynesia. They are all rather similar in morphology and coloration, but the nests of at least Atiu and Marquesan birds differ considerably. Medway (1975) uses similarities of nest structure as an argument for treating various Melanesian swiftlet populations as subspecies of *A. vanikorensis*, on the grounds that similarities in nest structure reflect similarities in genetically controlled behaviour patterns and in the cement-producing salivary glands. The different nests built by Atiu and Marquesan swiftlets may correspondingly imply that there are genetical differences in nest-building behaviour, but there is no evidence for differences in the salivary glands.

Mayr (1937) had earlier argued that certain swiftlet populations of generally similar appearance to *A. vanikorensis* should be treated as separate species merely because nearly all the other landbirds having similarly wide geographical ranges in the western Pacific Ocean were divided into several species. However, in advocating the merging of these populations into one species Medway (1975) pointed out that *Halcyon chloris*, for example, has as wide a range itself as the enlarged *A. vanikorensis* group. On the other hand nearly all the widespread land bird genera occurring on Atiu, Tahiti and in the

Marquesas Islands are represented by separate species in these three archipelagos. *Halcyon* for example, is represented by *H. tuta* on Atiu, *H. venerata* and a very small population of *H. tuta* on Tahiti and *H. godeffroyi* in the Marquesas Islands. However, the usefulness of general faunistic arguments of this kind in deciding particular cases is uncertain and it can easily lead to circular reasoning.

Gene-flow between the isolated swiftlet populations of Atiu, Tahiti and the Marquesas Islands is probably extremely infrequent, so that the question of species' taxonomic limits among them seems an artificial problem; moreover, the occurrence of sympatry of any of these three forms is remotely improbable so that the question will anyway remain unanswerable.

The most useful classification may therefore be one which expresses the above uncertainty, as follows:

- A. (leucophaeus) sawtelli* (Holyoak) Southern Cook Islands: Atiu;
- A. (leucophaeus) leucophaeus* (Peale) Society Islands: Tahiti; the small swiftlet population on Moorea and those formerly in the Leeward Society Islands (Thibault 1974) were presumably of this form;
- A. (leucophaeus) ocistus* (Oberholser) Marquesas Islands: Eiao, Nuku Hiva, Ua Huka, Ua Pou, Hiva Oa, Tahuata, Mohotani.

The use of a specific epithet placed in parentheses in this way was advocated 30 years ago by Kiriakoff (1948) for identifying closely related and often sympatric species, forming a group for which he coined the name 'ultra-species'. We prefer to restrict usage of such a system of brackets to closely related forms that represent each other geographically and with which the determination of species' taxonomic limits is little better than guesswork on present evidence.

Amadon (1966) advocated the use of a specific epithet in square brackets to identify particular species as components of superspecies and a specific epithet in parentheses to identify semispecies, which he defined as forms believed to be subspecies, 'but approaching, or possibly of, species status . . .'. Cain (1971) among others has pointed out the limitations and uncertainties inherent in the application of the superspecies concept and we do not wish to indicate that the three swiftlets listed above form a superspecies.

Treating all three Polynesian swiftlets in this way rather than as subspecies of *A. leucophaeus* should have the desirable effect of encouraging future workers to present biological information separately for each group of populations.

*Acknowledgements:* We are grateful to Linda Whitehouse for drawing the Figures and to John Bull for assistance in arranging photography at the American Museum of Natural History. The authorities of the A.M.N.H., British Museum (Natural History) and Museum National d'Histoire Naturelle kindly allowed access to specimens in their care. D.T.H. wishes to thank the Frank M. Chapman Memorial Fund of the A.M.N.H., the International Council for Bird Preservation, the Smithsonian Institution and the Winston Churchill Memorial Trust for funding, and J.-C.T. wishes to thank the International Council for Bird Preservation and the Académie des Sciences (Paris) for financial support. We are grateful to Lord Medway for helpful comments on our manuscript.

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## Bird skins from Malawi (formerly Nyasaland) in the Merseyside County Museums, Liverpool

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Received 5 November 1977

Benson & Benson (1977: 220-222), in notes on collections of bird specimens, in fact skins, from Malawi, give a total of c. 7,500 in the British Museum (Natural History) (BMNH) out of c. 16,000 in the world as a whole. They add that the only other museum in the United Kingdom holding any number of specimens is the University Museum of Zoology, Cambridge (UMZC), which obtained a share of a collection made by C. B. C. Storey in 1907, that is precisely 41 in the BMNH and 31 in the UMZC (Benson & Benson, *Arnoldia, Rhodesia* 7(32), 1975: 3).

As a result of an informal meeting of ornithologists with an African interest at the Merseyside County Museums, Liverpool (LIVCM) on 17 and 18 September 1977 ('The African Chat'), attended by all three of us, it became apparent that there was a very appreciable representation of material from Malawi in this museum, emanating from A. Whyte and Sir Alfred Sharpe. The Whyte material was included in Canon H. B. Tristram's first collection, purchased in 1896, while the Sharpe material was presented by Sir Alfred himself in 1903.